Growth behavior of *Phyllostachys nigra* var. *henonis* (Bambusoideae) in Central China

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Abstract: In the Shennongjia National Nature Reserve of Central China, the vegetative growth behavior of henon bamboo (*Phyllostachys nigra* var. *henonis* (Mitford) Stapf. ex Rendle) was studied from shoot recruitment to culm establishment. In May, bamboo shoots emerging from the ground achieved an average density of 2.7 shoots m^{-2} during the sprouting phase of 16 days. However, about 32% of the new shoots died back before maturity. Insect damage, withering death and rodent predation were responsible for 57%, 29 % and 14% of the total shoot mortality, respectively. From May to June, the shoots attained 400 ± 23 cm during the height growth phase of 34 days, with a daily rate varying from 1 to 56 cm. All branches and leaves unfolded during the branch spreading phase from June to August. Shoot production was positively related to the density of standing culms, but negatively to both coverage and height of herb layers.

Keywords: Bamboo shoot; growth; Henon bamboo; plantation, Shennongjia.

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Introduction

Before the advent of industrialization and cash-based transactions, bamboo had played an important role as a minor forest product in the self-sustaining economies of many nations that are now grouped together as developing countries, by providing food, raw material, shelter, and even medicine for millions of people (Tewari 1993; McClure 1993; Dransfield and Widjaja 1995; Quintans 1998). In recent years, bamboo has gained international recognition of its multiple uses and environmental benefits (Gielis 1998; Liese 2001; Diver 2001; Zhong *et al.* 2001). In China, bamboo plantation has increased by 30 % in the past two decades (Lei 2001). Meanwhile, bamboo export has increased from US$ 46.1 million in 1981 to US$ 300 million in 2000 (Lu 2001). In Australia, increasing consumption of bamboo shoots created a domestic market of US$ 10–20 million thus stimulating the establishment of bamboo plantations to supply fresh shoots in replacement of the imports, and also the development of an export market for fresh shoots to Asian countries during the Northern Hemisphere winter (Midmore 1997; Barnes *et al.* 1999). In North America, there is only one native bamboo species (i.e., *Arundinaria gigantea* (Walt.) Muhl.). However, about 441 kinds (species, subspecies, varieties, forms, and cultivars) of bamboo have been introduced in the USA since late 19th century (Shor 2002). No bamboo species is native to Europe, but currently over 400 varieties of bamboo are grown or cultivated in this continent (Gielis and Oprins 1998). An ongoing project, "Bamboo for Europe", is assessing the possibility of developing bamboo as an agroforest crop in European countries (Liese 2001).

The increasing importance of bamboo has led to a high demand for bamboo species which could be cultivated to alleviate agricultural and forestry problems - both environmental and socioeconomic - facing the world (Quintans 1998; Diver 2001). However, the actual research efforts spent on bamboo are highly imbalanced compared with that of other agricultural crops (Liese 1991; 2001; Shoch and Stoney 2001). For instance, knowledge on vegetative growth of bamboo, particularly on shoot sprouting and culm production, is important in defining the appropriate species that can be planted commercially and/or environmentally. To date, only a few species have been investigated.

Henon bamboo (*Phyllostachys nigra* var. *henonis* (Mitford) Stapf. ex Rendle) is a woody plant native to China (Keng and Wang 1996). Until the middle of the 18th century, it was the most common bamboo in Japan, and from there it was introduced in the West by Dr. Henon in 1895 as an ornamental plant (Cao 1989; Linvill *et al.* 2001). Almost every part of henon bamboo is usable. Its rhizomes are employed in making handicraft, while the culms are commonly used for handles of farm equipment, and as sunning poles, punt-poles and building material (Zhu *et al.* 1994). Strips from henon bamboo are pliable and tough and good for weaving, and the young shoots are delicious as a kind of special vegetable (Yi 1997). It is one of the most common bamboos dominating the mountainous areas in both subtropical and temperate China (Zhu *et al.* 1994). It can occupy much the same ecological niche as trees, and has many advantages over trees such as a relatively short time from planting to harvest and the ability to provide products sustainably for over six decades without damaging its vegetative regeneration (Fu and Banik 1995).

In the Shennongjia National Nature Reserve (SNNR hereafter) of Central China, henon bamboo grows from mountain feet (ca. 500 m) up to 1840 m (Ban *et al.* 1995), adapting to environmental condition with annual average temperature ranging 7–14 ℃, and average annual precipitation of 700–1700 mm (Zhu and Song 1999). Given the ability to adapt to wide environmental condi-

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tions, henon bamboo could be introduced to most temperate regions of the globe as a new crop. In fact, small-scale growers in the USA had already successfully created shoot-oriented plantation of this species in recent years (Lewis 1998; Miles *et al.* 2000). This study is aimed at understanding bamboo growth in terms of sprouting, shoot survival, and height growth.

Material and methods

The species

Henon bamboo differs from the original species *Phyllostachys nigra* (Lodd. ex Lindl.) Munro, in the culm, which does not turn dark purple and is taller and thicker (Keng and Wang 1996; Yi 1997). Mature culms of henon bamboo often reach more than 5 m, sometimes up to 10 m, and diameters at breast height (DBH) range from 2–6 cm. New shoots, tightly wrapped with brown sheaths, emerge annually from lateral buds on rhizomes that are below ground at a depth of about 0-30 cm. Its vegetative growth, like other woody bamboos, comprises of three successive phases, i.e., shoot sprouting (new shoots emerging from the ground), height growth (emerged shoots elongating and growing to full height), and branch spreading (Liese 1985; McClure 1993; Dransfield and Widjaja 1995). Accordingly, understanding the dynamics of these three phases is an essential step to appraise its plantation.

Study site

The study was carried out between March and August 2001 within a 0.25 hm^2 semi-wild bamboo stand (N31°28'762", E110°23'127", ALT. 1290–1310 m) near Muyu, the capital town of SNNR, Hubei Province of Central China. The bamboo grove was planted 45 years ago and has not flowered since the plantation. Its management consisted of annual shoot harvesting and pole cutting only. Climate of the region is a warm-temperate with warm, rainy summers and cool, dry winters. The average annual temperature is 11.2 °C, with a monthly maximum of 22.8 °C in July and a monthly minimum of 0.7 °C in January. Annual precipitation is about 1150 mm, with 86% of rainfall during the growing season from April to October (Zhu and Song 1999). A soil profile from the bamboo stand shows that the organic fraction of horizon A_0 (0–4 cm) was dominated by bamboo leaves (> 70 %). Horizon A (4–18 cm) was formed by grayish-yellow loam with moderate acidity (pH 6.0), while horizon B (18–45 cm) consisted of a more acid (pH 5.5) clayey-loam, purplish-yellow in color. Horizon BC occurred below 45 cm and was reddish-yellow in color.

Field observation

For regular observation of the bamboo growth, five 2m×5 m plots were set up inside the bamboo stand in early March 2001. The community features of the standing bamboo, i.e., culm density, culm height, culm DBH, number of culm nodes, and culm age were measured in each plot in March. Height and coverage of the herb layer under the bamboo canopy were assessed in late April when herbs were well developed. Growth monitory was focused on the sprouting; survival, and height growth of the new shoots. During the sprouting phase, shoot emergence was daily inspected in all plots from April to May. Shoots were considered sprouted when they were 3 cm above ground. Then, the individual then shoot was tagged and its emerging date, initial height, base diameter were recorded. Survivorship of each tagged shoot was continuously monitored throughout the study period. Shoots were considered lost when they feed were by animals, damaged by insects, or withered before maturity. During the height growth phase, ten shoots were selected and their height growth were measured daily at around 8.00 a.m., until their full height.

Data analysis

Emergence of new shoots through the sprouting phase was expressed as both daily sprouting (daily emergence of new shoots) and cumulative sprouting (cumulative emergence of new shoots). The *t*-Test was used to assess whether daily sprouting follows a normal distribution pattern or not. If so, the sprouting phase was then divided into three successive periods: one period in the mid-phase and two periods, respectively, at the beginning and the end of the phase. A logistic model was adopted to describe the relative cumulative sprouting. In the model, the upper boundary is replaced by the maximum relative value of the cumulative sprouting, i.e., 100% at the end of the sprouting phase. Therefore, the modified model takes the form as: $S = 1 / [1 / 100 + a \times b^T]$, where S is the percentage of cumulative sprouting; a and b are fitted parameters; and T is the time in the sprouting phase expressed in days. Linear models were adopted to determine the relationship between the thickness (base diameter) of the shoot and the time of its emergence, as well as the relationship between the base diameter of the shoot in spring and its full height in autumn. Height growth was expressed relative to the final height recorded. Cumulative growth of shoot height through the height growth phase was also described with the logistic model. Paired samples analysis was used to test the effects of bamboo community features on the production and survivorship of the new shoots. All calculations were carried out on SPSS for windows 10.0.

Results

Community features

Vertical structure of the bamboo community was quite simple: pure bamboo as the upper canopy and herbs as the ground layer. The bamboo layer was 3–5 m high and covered 80%–100% of the plot area, with an average density of 7 ± 2 culms m^{-2}. The herb layer covered 7%–35% of the ground. In the stand, bamboo culms were 411±74 cm high and 14±2 mm thick in DBH. Age structure of culms in four age classes, i.e. 1-2-3-4(+) years of age, shows a ratio of 1:1.1:1.3: 0.9 in the stand (Table 1).

Table 1. Features of henon bamboo (*Phyllostachys nigra* var. *henonis*) communities in the Shennongjia National Nature Reserve, China

Plot	A	B	C	D	E	Mean± S.D.
Age structure						
Total culms	69	103	43	64	89	73±24
1-year old culms	11	22	9	14	29	17±8
2-year old culms	23	21	14	19	20	19±3
3-year old culms	18	33	11	20	26	22±8
4(+)-year old culms	17	27	9	11	14	16±7
Culm features						
Mean height (cm)	367	411	321	516	441	411±74
Base-area ground cover (%)	0.16	0.29	0.04	0.18	0.22	0.17±0.09
Mean DBH (mm)	14.1	15.7	10.1	15.8	14.5	14.0±2.3
Mean number of nodes	25	24	18	26	25	24±3
Herb layer						
Coverage (%)	7	21	34	23	20	21±10
Height (cm)	15	10	20	15	10	14±4

Each plot covers an area of 10 m²

Shoot sprouting

A total of 137 bamboo shoots emerged from the ground in five 2m×5 m plots from 9 to 27 May, with an average sprouting rate (ASR) of 7.2 shoots day^{-1}. The sprouting phase lasted 16 ± 2 days, and the new shoots achieved average density of 2.7 ± 0.9 shoots m^{-2} at the end of the phase. The daily sprouting was not even throughout the sprouting phase, but significantly followed a normal distribution (t_{18} = 5.37, P < 0.001). Thus the sprouting phase can be divided into three successive periods: initial sprouting period (a period with sprouting rate lower than ASR at the beginning of the sprouting phase), full sprouting period (a period with sprouting rate higher than ASR in the mid phase), and final sprouting period (a period with a sprouting rate lower than ASR at the end of the phase). The initial sprouting period lasted 6 days (9–14 May) and contributed 15% of the newly emerged shoots; the full sprouting period lasted 7 days (15–21 May) and contributed 72%; the final sprouting period lasted 6 days (22-27 May) and contributed 13% (Fig. 1). Cumulative sprouting percentage significantly followed a logistic model: $S = 1 / (1 / 100 + 1.62 \times 0.5679^T)$ (P < 0.001).

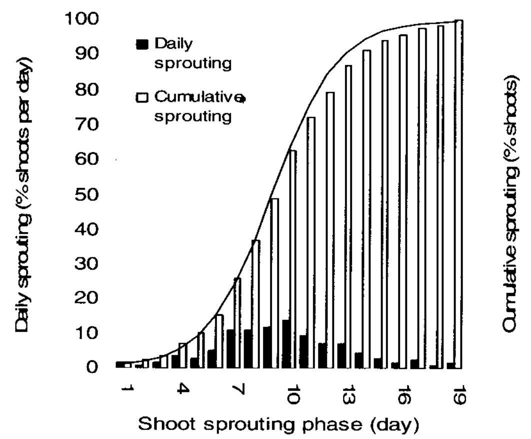

Fig. 1. Shoot emergence of henon bamboo (*Phyllostachys nigra* var. *henonis*) in the growth season of 2001 in the Shennongjia National Nature Reserve, Central China. Daily sprouting percentage throughout the sprouting phase significantly follows a normal distribution pattern (t_{18} = 5.368, P < 0.001). Cumulative sprouting percentage (S) follows a logistical model as: $S = 1 / (1 / 100 + 1.62 \times 0.5679^T)$ (T indicates the time with the first day of the sprouting phase = 1, r^2 = 0.920, F-value = 196, P < 0.001).

The thickness (i.e., base diameter) of the bamboo shoot was strongly (r = - 0.978) related to its emerging order (Fig. 2). This finding implies that the bigger buds had gathered more nutrients from the rhizomes before they emerged, so that during the sprouting phase they could grow more quickly than the small ones. The thickness of the shoot in spring significantly (r = 0.902) determines its full height in autumn (Fig. 3).

Shoot survival

Survival rate of new shoots did not differ significantly between plots, which was around 68±5% (Table 2). Insect damage, withering, and rodent predation were responsible for 57%, 29% and 14% of the total shoot loss, respectively. The new shoots were mostly susceptible to rodents during the first two weeks, and to insects (weevils) during the first six weeks. Withering death mainly occurred on the shoots that emerged during the final sprouting period. The thinner shoots had a higher mortality rate. Mortality rate of shoots with a base diameter below 16 mm was 56%, while that of shoots with a base diameter above 18 mm was only 20%.

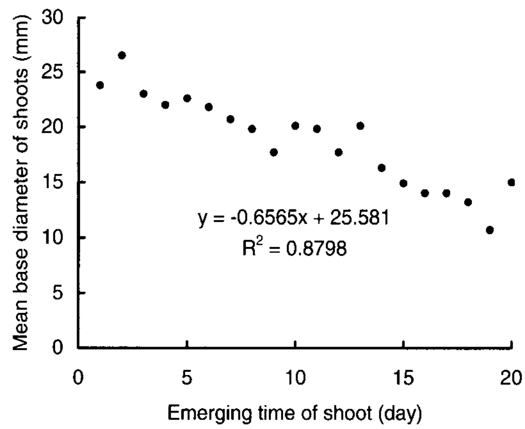

Fig. 2 Relationship between basal diameter of henon bamboo (*Phyllostachys nigra* var. *henonis*) shoots and their date of emergence in the Shennongjia National Nature Reserve, Central China. In the equation, Y indicates the base diameter of the shoot and X its emerging day with the first day of the sprouting phase = 1 ($d.f.$ = 17, F-value = 153, P < 0.001).

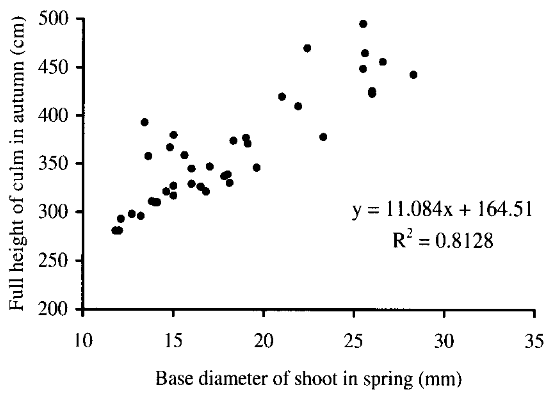

Fig. 3 Relationship between base diameter of henon bamboo (*Phyllostachys nigra* var. *henonis*) shoot in spring and its height in autumn in the Shennongjia National Nature Reserve, Central China. In the equation, Y indicates full height of bamboo shoot in autumn and X its base-diameter in spring ($d.f.$ = 39, F-value = 119, P < 0.001).

Table 2. Emergence and mortality of new shoots of henon bamboo (*Phyllostachys nigra* var. *henonis*) in the Shennongjia National Nature Reserve, Central China

item	plot					Total	Mean±S.D
	A	B	C	D	E		
Shoots emerged	28	37	18	19	35	137	27±9
Shoots lost	9	11	7	6	9	42	8±2.
Insect damage	5	6	5	4	4	24	5±1
Withering death	3	2	2	0	5	12	2±2
Animal predation	1	3	0	2	0	6	1±1
Survival rate %	68	70	61	68	74	69	68±5

Each plot covers an area of 10 m^2

Observations revealed that herbs, in terms of ground cover and mean height, negatively affected the shoot survival. Herb height strongly reduced the shoot survival rate (r = -0.939, P < 0.01). The effects from herb coverage were not as strong as from herb height, although herb coverage also negatively influenced the shoot survival rates (r = –0.535).

Height growth

The new shoots grew to their full height of 400±23 cm (n = 40) in the height growth phase of 34 ± 2 days (n = 10). The daily growth varied from 1 to 56 $cm \cdot d^{-1}$ with an average growth rate (AGR) of 12.4±0.9 $cm \cdot d^{-1}$. This growth phase started in May after the emergence of the shoot and was completed in early July. It was observed that height growth presented a slow-fast-slow sequence, which was identified by plotting AGR against time during the growth phase. An initial slow-growth period lasted 10 ± 1 days with a mean growth rate of 5.0±0.6 $cm \cdot d^{-1}$. Thereafter, growth accelerated to over a period with growth rate higher than AGR in the mid phase, which lasted 21 ± 2 days with a mean growth rate of 20.9±2.1 $cm \cdot d^{-1}$. At the end of the fast-growth period, culm sheaths at the base nodes began to fall and branches started to spread, which made growth slow down. The final slow-growth period lasted 8 ± 2 days with a mean growth rate of 5.1±1.1 $cm \cdot d^{-1}$. The relative cumulative growth of bamboo shoot followed a logistic model (Fig. 4): $H = 1 / (1 / 100 + 1.039 \times 0.779^{T})$, where H indicates the percentage of cumulative height of the shoot. The branch spreading phase lasted from the final slow-growth period in mid-June until early August. At the end of branch spreading phase, the new culms are formed when all culm sheaths have fallen and all branches are unfolded. Thereafter, height, diameter and volume of the culms are stable and do not change noticeably.

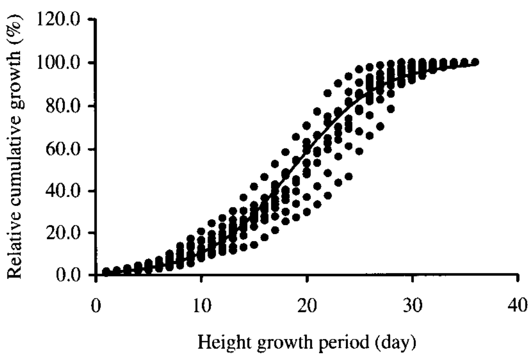

Fig. 4. Relative accumulative growth of henon bamboo (*Phyllostachys nigra* var. *henonis*) from shoot emergence until full height of 10 sample shoots in the Shennongjia National Nature Reserve, Central China. Growth process can be described with a logistic model as: $H = 1 / (1 / 100 + 1.039 \times 0.779^{T})$ (r^2 = 0.993, F-value = 4685, P < 0.001). H indicates the percentage cumulative height of the shoot and T the time with the first day of the height growth phase = 1.

Discussion

Shoot sprouting and growth

In seasonal climates, bamboo, like other plants, grows in a regular annual cycle (Liese 1985, McClure 1993). It seems that all woody bamboo species follow a three-phase growth sequence. Firstly, a young shoot emerges from the ground. It consists essentially of a short, little-differentiated stem protected by numerous sheaths. This new shoot develops slowly at first, but elongates rapidly in the mid-phase and grows to full height after a slow down period. Finally, branches are unfolded and a culm has then established. However, the length of each phase varies from species to species (Table 3), depending on the rhizome structure of the bamboo.

There are two basic types of rhizomes: sympodial (clumping bamboo) and monopodial (running bamboo) (McClure 1993). Sympodial bamboos have short thick rhizomes and their new shoots directly come from distal ends of the rhizomes. Monopodial bamboos have long adventitious rhizomes that are cylindrical and segmented like the culms. Therefore, new shoots of the monopodial bamboo come from the lateral buds of the rhizomes. Studies have shown that the monopodial bamboo sprouts and grows much quicker than the sympodial bamboo (Table 3). Shoots of *Phyllostachys* bamboo (monopodial, 6 species) usually emerge in spring and early summer within a short sprouting phase averaging 30±10 days. Emerged shoots rapidly elongate and form a canopy of the stand within 40±15 days. Clumping bamboos (sympodial, 5 species from the genera of *Fargesia*, *Dendrocalamopsis* and *Dendrocalamus*) usually have much longer sprouting (106 ± 47 days) and elongation (102±37 days) phases.

The onset and length of the sprouting phase are important aspects of vegetative growth used to assess the economic potentials of bamboo species. Henon bamboo is one of the rapidly sprouting (19 days) and fast growing (32–36 days) bamboos. Farmers appreciate henon bamboo because each year they only need to spend two weeks harvesting shoots in spring and another two weeks for weeding and cutting old culms in winter. Furthermore, edible shoots of henon bamboo come out in April-May, a slack season of fresh vegetable supply in Central China, thereby benefiting the bamboo farmers every year. However, the sprouting phase may vary with the ambient environmental conditions. For instance, in subtropical China, the sprouting phase of *Phyllostachys pubescens* has been observed to take 28–31 days (Zhang *et al.* 1995; Zheng *et al.* 1998a), while in temperate South Carolina, the USA, its takes as long as 44 days (Lee and Addis 2001). Further observations on henon bamboo are thus needed in other habitats, e.g., South and East China, to select suitable ecological types for matching the different purposes of plantation.

Shoot production

It is thought that the structure of the bamboo community strongly affects the production of new shoots since the mature culms are the only nourishing source for the new shoots (Liese 1985). In our henon bamboo stand, the annual production of bamboo shoots strongly depends on density (r = 0.938) and coverage (r = 0.826) of the standing culms. The results confirm the nourishing role of the mother culms. Mother culms contribute to the vegetative growth of the clump through photosynthesis in their leaves. The carbohydrates they synthesize are partly utilized by the culms themselves, but a greater proportion is transported to the rhizomes (Fu 1989; 1992; Qiu *et al.* 1992; Isagi *et al.* 1997). Here they are stored as energy resources for the next year's growth of new shoots. Consequently, the bamboo farmers are often faced with a problem of how many shoots should be left in their bamboo stands. If all shoots are harvested, the bamboo clumps will lose vigor and production; if all shoots are left, the farmers will lose money and food.

This problem has been discussed for *Phyllostachys pubescens* in Japan (Watanabe 1994) and China (e.g., He 1993; Zheng *et al.* 1998) for many years. M. He (1993) suggested an age-rotation model for maintaining shoots in the timber-oriented stands as follows: Culms in 1-2-3-4(+) age classes = 1:1:1:1, while Zheng *et al.* (1998b) modified the ratio as 1:1.6:1.6:1.5 for the shoot-oriented clump. However, what ratio should be set for optimal both bamboo shoot and culm yield is unknown yet. In the present study, the age structure of henon bamboo was 1:1.1:1.3:0.9 (Table 1), approximately the optimal age ratio for the culm-oriented plantation. Considering that the productivity of this henon bamboo stand was 1.9 culms·m^{-2}·a^{-1} (Table 1), and the number of emerging shoots was 2.7 shoots·m^{-2} (Table 2), the cashable shoot yield of this stand could be expected to be 0.8 shoot·m^{-2}. Of course, farmers can adjust the harvest ratio of bamboo shoots according to market variation and stand conditions.

Table 3. Length of sprouting phase and height growth phase of selected Chinese bamboos

Species	Rhizome type	Stand location	Sprouting phase (days)	Growth phase (days)	Source
Spreading/running bamboo					
Phyllostachys pubescens	Mono	S. China	31	NA	Zheng *et al.* (1998)
Ph. pubescens	Mono	E. China	28	33	Zhang *et al.* (1995)
Ph. pubescens	Mono	USA	44	70	Lee and Addis (2001)
Ph. nigra	Mono	E. China	27	24	Zhang *et al.* (1997)
Ph. makinoi	Mono	E. China	25	32	Huang and Ma (1994)
Ph. heteroclada	Mono	E. China	45	39	Jin *et al.* (1999)
Ph. nidularia	Mono	W. China	20	45	Zhang *et al.* (1995)
Ph. nigra var. *henonis*	Mono	C. China	19	34	This study
Clumping bamboo					
Fargesia robusta	Sym	W. China	80	70	Qin *et al.* (1993)
F. denudata	Sym	W. China	90	163	Wang *et al.* (1991)
F. spathacea	Sym	C. China	59	110	Li (2003)
Dendrocalamopsis oldhami	Sym	S. China	120	80	Gao *et al.* (2000)
Dedrocalamus latiflorus	Sym	E. China	180	90	Zhou (1999)

Note: In the table: Mono = Monopodial rhizome, Sym = Sympodial rhizome, NA = No data available.

Bamboo stand management

The management of the henon bamboo includes two important aspects: shoot harvest and site control. Various kinds of diseases and damage affect bamboo shoots during their different growth phases. In the plots, damage through animal predation mainly occurred in the sprouting phase, whereas withering death mainly occurred among later shoots. Corresponding to this mortality pattern, both early and late emerged shoots could be harvested as vegetable before they are damaged. For edible bamboo shoots, however, the shoots must be harvested as soon as they emerge. Even waiting a day will make them undesirable and unsavory for eating since exposure to sunlight causes the production of chemicals that are bitter, and hastens shoot elongation by stimulating the development of woodiness (Lewis 1998).

Weeding should be considered as a key issue, as our findings present that the herbs in the bamboo stands were strong negative to the shoot production as well as shoot survival rate. Generally, weeds absorb nutrients intended for the bamboo, shade the ground, lower soil temperature and thus retard shoot emergence (Fu 1994). In the field, such negative effects were increased by taller herbs which may be competing with bamboo roots for water and nutrients in the deeper soil. Therefore tall herbs should be removed from the bamboo stands.

In conclusion, the management of bamboo systems is necessary to sustainable productivity. For henon bamboo, the following recommendations are derived from this study: 1) In order to manage the bamboo stand for both shoot and culm, the bamboo culms in 1-2-3-4(+) years of age class in the culm-oriented stands should be controlled around 1:1:1:1. In the henon bamboo stand, an average of 1.9 new shoots·m^{-2} should be allowed to grow into culms. Any additional ones (0.8 shoot·m^{-1} in this case) could be harvested each year. 2) Shoot harvest should be more concentrated on early and late emerging shoots since they suffer from animal predation and scarce rhizome reserves respectively. 3) Standing culms should not be completely felled under any circumstances, but tall herbs with deep roots should be removed from within the bamboo stand.

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